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Environmental Conservation

DOI:
10.1017/S0376892915000284

Published: 01/06/2016

Peer reviewed version

LONG-TERM MODIFICATIONS OF COASTAL DEFENCES ENHANCES DIVERSITY BY MODIFYING NETWORKS OF INTERACTIONS

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Wordcount: 6057

SUMMARY

Realisation that hard coastal defence structures support lower biodiversity than natural habitats prompted a wealth of research seeking to identify design enhancements that offer ecological benefits. Some studies showed that artificial structures could be modified to increase levels of diversity. The majority of studies, however, have only considered the short-term effects of such modifications even though reliance on results from short-term studies may lead to serious misjudgements in conservation ecology. In this study, we planned a long-term 7-year experiment to examine how the addition of small pits to otherwise featureless seawalls could enhance the stocks of a highly exploited limpet (*Patella candei*). Modified areas of the seawall supported enhanced stocks of limpets 7 years after the addition of pits. Modified areas of the seawall also supported a community that differed in the distribution of littorinids, barnacles and macroalgae compared to the controls. Responses to the different treatments (varying in the numbers and size of experimental pits) were species-specific and there was evidence that some species responded directly to differences among treatments, whereas others responded indirectly via changes in the distribution of competing species. This type of habitat enhancements is easily done and can have positive long-lasting effects on the ecology of urban seascapes. Understanding the interactions between species can lead to a rule-based approach to interventions to enhance biodiversity.

Keywords: Azores, coastal urbanisation, community structure, conservation, habitat enhancement, long-term, *Patella*

INTRODUCTION

The replacement of natural shores by hard coastal defence structures (e.g. seawalls, breakwaters, revetments, groynes) is increasing as a response to the growing need to defend the coast from sea level rise and stormier seas (e.g. Airoldi *et al*. 2005; Moschella *et al*. 2005; Chapman 2006). Realisation that these structures generally support lower biodiversity than natural habitats (e.g. Chapman 2003; Chapman 2006; Chapman & Bulleri 2003; Moschella *et al*. 2005; Vaselli, Bulleri & Benedetti-Cecchi 2008; Firth *et al*. 2013a; Browne & Chapman 2014) has focused attention on designing structures that help facilitate specific ecological outcomes (Firth *et al*. 2014).

In cases where natural shores are completely replaced by artificial habitats there will be an obvious loss of habitat and the species therein. However, even when species colonise such artificial structures, they can hardly be considered as surrogates for the natural shores they replace (see review by Chapman & Underwood 2011). For instance, there is now documented evidence that on such hard coastal defence structures (e.g. seawalls) there can be changes in the composition of species assemblages (Bulleri *et al.* 2005; Moschella *et al.* 2005), abundances (Chapman 2003), size-structure and reproductive output of populations (Moreira *et al.* 2006) and competitive interactions (Jackson *et al.* 2008; Iveša *et al.* 2010). Moreover, less obvious changes in community structure can also be found on natural shores surrounded (Goodsell *et al.* 2007) or in the vicinity (e.g. Martins *et al*. 2009) of such artificial habitats.

Lack of habitat heterogeneity has been put forward as the main cause of the lower level of biodiversity generally observed on sea defence structures (Chapman & Underwood 2011). There is now mounting evidence that experimentally increasing the complexity and heterogeneity of otherwise topographically simple surfaces, for example by including water-retaining features, pits and crevices, can substantially increase the biodiversity of the structure (Chapman & Blockley 2009; Firth *et al*. 2013b; Browne & Chapman 2014; Firth *et al*. 2014). Modifications can also be tailored to increase the abundances of species of economic interest (Martins *et al*. 2010). These studies generally support the idea that hard coastal defence structures can be modified to support an increasing level of diversity and thus contribute toward the conservation and management of urbanised coastlines whilst providing effective protection from sea level rise and stormier seas.

A common feature of these studies, however, is that they are relatively short-term (typically < 1 year, e.g. Martins *et al*. 2010; Browne & Chapman 2014) and little is known about how modifications made to coastal defence structures continue to influence community structure in the longer term. This is important as there is evidence that results from short-term experiments do not always mirror those in the longer-term (e.g. O'Connor & Crowe 2005) and that this may have important implications when considering management actions (Callahan 1984; Magnuson 1990).

Patella candei d'Orbigny is an endemic species to the Macaronesia where it is extensively exploited for human consumption. In the Canary Islands, for

instance, *P. candei* is virtually extinct, presumably to due to over-exploitation
102 (Côrte-Real *et al*. 1996; Navarro *et al.* 2005). In the Azores, *P. candei* has
also been historically collected with an important input to the local economy
104 until the collapse of the stocks in the mid 1980s (Hawkins *et al.* 2000). The
decline in limpet abundances is arguably the largest anthropogenic impact on
106 Azorean coastal ecosystems and has been correlated with archipelago-wide
ecological impacts including changes in the balance between consumers and
108 producers (Martins *et al.* 2008). In 1993, legislation has been passed
establishing fishing protected zones (where the collection of limpets is fully
110 prohibited), seasonal fishing closures and minimum legal catch sizes. Such
measures, however, have proved largely unsuccessful due to lack of
112 enforcement and populations of limpets are currently still showing clear signs
of over-exploitation (Martins *et al*. 2011).
114
In 2006, experimental habitat enhancements, consisting of the addition of pits
116 differing in size drilled into seawalls at different densities, showed that over
the short-term (4 months) the abundance of limpets increased in enhanced
118 areas of the seawall (in comparison to unmanipulated controls) as a result of
both animal immigration and new recruitment (Martins *et al.* 2010). Results
120 showed that the overall effects of pit density and size varied with limpet size
class with the numbers of large limpets being limited by the availability of pits
122 of the larger size, whereas small limpets were limited by the density of pits (of
whatever size). In this study we re-surveyed the experiment after 7 years to
124 evaluate the long-term effects of experimental habitat enhancement on the
abundances of the limpet *P. candei*.

As well as their economic value in some parts of the world, patellid limpets also play a key community structuring role on European shores (e.g. Hawkins & Hartnoll 1983; Jenkins *et al*. 2005; Coleman *et al*. 2006), suggesting that variation in the distribution of limpets as a response to different habitat enhancements may have led to community-wide cascading effects. Moreover, different species of grazing gastropods have distinct influences on the community (e.g. Hawkins *et al*. 1989; O'Connor & Crowe 2005; Griffin *et al*. 2010). A 7-year period was judged long enough to allow the full influence of changes in habitats on the establishment of networks of interactions (e.g. competition, facilitation, predation).

METHODS

Study sites and community

The study was done at São Roque on the island of São Miguel, Azores. São Roque was a gentle sloping basaltic rocky shore with a large number of rock pools that has been largely replaced by the construction of a 4-5 km long seawall for protection of the shoreline. Our experimental habitat enhancement was applied to a seawall made of 2 m wide natural basaltic blocks; these had smooth surfaces and lacked the micro-topographic rugosity characteristic of adjacent natural shores (Martins *et al*. 2010). The experimental treatments were applied at mid shore level just above the algal dominated lower shore in areas where the barnacle *Chthamalus stellatus* is the dominant space occupier and the limpet *Patella candei* reaches its largest abundance. Other patellid limpets (*P. aspera*) present on Azorean shores are not common at this

tidal height. At this height, macroalgae are generally restricted to ephemeral species (e.g. *Ulva* spp., *Chaetomorpha* spp.) and a few perennial turf-forming algae (e.g. *Caulacanthus ustulatus*). Other grazing gastropods, including the littorinids *Tectarius striatus* and *Melarhaphe neritoides*, can also be locally abundant.

At each of two sites 200 m apart, 25 areas of 25 × 25 cm were marked and randomly assigned to 5 treatments. Five replicate areas were assigned to unmanipulated controls. The remaining 20 areas were randomly assigned to a 2-way orthogonal design including the factors pit size (small and large) and pit density (high and low) with five replicates per treatment. Small and large pits were 12 and 24 mm in diameter (both with a depth of 10 mm). Lesser and greater density treatments corresponded to 8 and 16 pits drilled within each area. Pits were drilled using an electrical power drill and were evenly spaced within the experimental areas. The sizes and densities of pits used are within the range of sizes and densities of pits observed on natural shores (for further details see Martins *et al*. 2010). The experimental habitat enhancement was established between November and December 2006.

Sampling design

Experimental areas were resurveyed in November 2013 (84 months after establishment) and March 2014 (87 months after establishment). During the period of time between the start of the experiment and the initial sampling to determine short-term effects of habitat enhancements (see Martins et al. 2010) and the resurveys in 2013 and 2014, the experimental areas were left

176 untouched and no sampling occurred. In November 2013, experimentally enhanced plots were re-located and assessed for signs of deterioration (e.g. 178 experimental treatments, i.e. number and size of pits, were still evident and not masked by natural erosion). At this time, the abundance of mobile 180 gastropods (*Patella candei*, *Tectarius striatus* and *Melarhaphe neritoides*) within each area (25 x 25 cm) was counted. Control areas were not evaluated 182 and sampled at this time. In March 2014, we resurveyed the experiment and recounted all gastropods including those in control areas. In addition, we 184 estimated the percentage cover of sessile species (macroalgae and barnacles). For this purpose, we used a 25 $\times$ 25 cm sampling quadrat divided 186 in 25 sub-quadrats. Within each sub-quadrat, a score between 0 (absent) and 4 (full cover) was attributed to all species present. Total percentage cover was 188 obtained by summing the scores of the 25 subquadrats (see Dethier *et al*. 1993 for further details). Mobile animals (limpets and littorinids) were counted 190 as described above, and limpets were measured (shell maximum length) using a Vernier calliper. We were able to find all areas except 3 control 192 locations (marks were gone). We replaced these missing controls with 3 randomly selected areas scattered among experimental areas. No attempt 194 was done to sample communities surrounding the experimental areas (25 x 25 cm) since the strongest interacting species in this system, *P. candei*, 196 exhibits a homing behaviour (Cacabelos unplished data) and was thus unlikely to influence assemblage structures a few centimetres away from the 198 experimental areas.

200 **Data analysis**

Enhanced vs control areas

To test the hypothesis that experimentally enhanced areas (no matter the treatment) support a greater abundance of limpets and a community structure that differs from unmanipulated controls, we used a 2-way mixed model PERMANOVA (a permutational-based analysis of variance, Anderson 2001) with the following factors: site (2 levels, random) and treatment (2 levels: enhanced treatments vs controls, fixed). We used the contrast function, which makes a partition of the variance and allows the comparison of the variable of interest among controls and the experimentally enhanced areas as a whole (a similar approach to that used in an asymmetrical analysis). The variables analysed were the abundance of the gastropods (*Patella candei*, *Tectarius striatus* and *Melarhaphe neritoides*) and the percentage cover of the barnacle *Chthamalus stellatus* and macroalgae. Prior to analysis, macroalgae were grouped into two morpho-functional groups: uncorticated ephemeral algae including both filamentous (*Chladophora* spp.) and foliose (*Ulva* spp.) species; hereafter referred to as ephemerals alone) and corticated perennial turfs (e.g. *Caulacanthus ustulatus*; hereafter referred to as turfs alone). Encrusting algae were also present in some areas, but their overall abundance was very low (< 1%) and was not analysed. This analysis was applied to data sampled on March 2014 as no controls were sampled during November 2013.

Comparison among habitat enhancement treatments

To test the hypothesis that different enhancement treatments (variation in pit density and size) influence the distribution of limpets leading to community-wide differences we used a 3-way PERMANOVA design with the following

226 factors: site (2 levels, random), pit size (2 levels, fixed) and pit density (2 levels, fixed). The analyses were run to test for differences in the abundance
228 of all three gastropods species in November 2013 and March 2014. Results were similar between these two dates and we only present data from March
230 2014 for simplicity (analysis of November 2013 in supplementary online material 2). These analyses were also run to test for differences in percentage
232 cover of barnacles and macroalgae (turfs and ephemerals).

234 All the univaritate analyses were run using the routine PERMANOVA (Anderson 2001) available on PRIMER V6 (Clarke & Gorley 2006) based on
236 Euclidean distances and using 999 permutations of residuals under a reduced model (similar to traditional ANOVA). Prior to analyses, data were checked for
238 heterogeneity of variances using the PERMDISP (Anderson 2004) function and transformations were applied where necessary (Underwood 1997). Pair-
240 wise comparisons were done to test for differences among means within significant terms.
242
The chi-squared test of independence (or association) was used to test the
244 null hypothesis of no association between the frequency of the three species of grazing gastropods and the experimental treatments. The mean number of
246 each species in each of the four treatments was used as observed frequencies, respectively.
248

We used Pearson's product-moment correlation to highlight potential relationships emerging from changes in the abundance of grazers on the sessile taxa.

RESULTS

Enhanced vs control areas

Analysis of the gastropod assemblages showed that all the three species (*Patella candei*, *Tectarius striatus* and *Melarhaphe neritoides*) tended to be more abundant in enhanced areas of the seawall compared to unmanipulated controls (Fig. 1 A-C). This result was significant in the cases of *P. candei* and *T. striatus* (Table S1 - Appendix ST1), which were around 5 and 11 times more abundant in enhanced areas of the seawall, respectively. Although the abundance of *M. neritoides* was over 2 times greater in enhanced areas of the seawall (Fig. 1C), no significant effect of seawall modification was found (Table S1). The mean limpet biomass per plot (dry body weight estimated for each individual from an established length-mass relationship, see Martins et al., 2008) of *P. candei* was also approximately 5 times greater (mean limpet biomass in mg $\pm$ SE, control: 38.2 $\pm$ 17.2, enhanced areas: 182.9 $\pm$ 30.4) in enhanced areas of the seawall. When considering the entire grazing assemblage (all species together), there was a significantly greater number of grazers in enhanced areas of the seawall than in unmanipulated controls (Fig. 1D, Table S1 - Appendix ST1).

The abundance of barnacles and turfs was greater in enhanced areas of the seawall (Fig. 2A,C), although this was only statistically significant in the case

274 of barnacles (Table S2 - Appendix ST1). The abundance of ephemerals was highly variable among areas and there were no differences observed in the
276 comparison between enhanced and control areas (Fig. 2E, Table S2 - Appendix ST1).
278

Comparison among habitat enhancement treatments

280 Species making up the gastropod assemblage had variable responses to the different treatments. The limpet *P. candei* responded positively to both the
282 density and size of pits (Fig. 3A), being significantly more abundant in enhanced areas with a higher density of pits and in areas with larger pits
284 (Table S3 - Appendix ST1). In contrast, the littorinids *T. striatus* and *M. neritoides* did not respond to pit density, but were significantly more abundant
286 in areas of the seawall enhanced with small pits (Fig. 3 B-C, Table S3 - Appendix ST1). For *M. neritoides* this result was only detected at one of the
288 sites examined.

290 Overall, the null hypothesis of no association between the gastropod assemblage and the experimental treatments was rejected (Table 1). This
292 result suggests that each enhancement treatment supports a structurally divergent assemblage of grazers (Figure 3D). This was especially evident in
294 those treatments that differed the most (small pit size and low density vs large pit size and high density) - as indicated by the relative chi-squared
296 contribution of each treatment (Table 1). All the above patterns were also present and similar 4 months earlier in November 2013 (Appendix S2)
298 suggesting that this pattern was temporally consistent.

When considering the remainder of the assemblage, the abundance of barnacles tended to be greater in areas with large pits (Fig. 2B), although this was not statistically significant (Table S4 - Appendix ST1). A significant interaction between site, pit density and pit size was detected in the case of turfs (Table S4 - Appendix ST1). Pair-wise comparisons showed that the abundance of turfs was similar among areas with small and large pits, but was significantly greater in areas with higher pit density (Fig. 2D), at site 1 (Table S4 - Appendix ST1). The abundance of ephemerals also varied among enhancement treatments (Fig. 2F). A significant interaction was found between site and pit density (Table S4 - Appendix ST1). The abundance of ephemerals was greater in areas with lower pit density (Fig. 2F), although this was only significant at site 1 (see pair-wise comparisons in Table S4 - Appendix ST1).

Strong correlations were found between the abundance of barnacles, turfs and ephemerals and *P. candei* (Table 2). The correlation was positive for barnacles and turfs, but negative between ephemerals and limpets. The abundance of barnacles and ephemerals was also weakly positively correlated with *T. striatus* but there was a strong and negative correlation between the later and the abundance of turfs (Table 2). All the sessile taxa (barnacles, turfs and ephemerals) showed a negative correlation with the abundance of *M. neritoides* (Table 2).

DISCUSSION

Long-term effects on the target species

Our results suggest that those areas of the seawall that were experimentally modified to enhance the abundance of the highly exploited limpet *Patella candei*, have had a long-term impact. Although no sampling was done in between the two periods, our resurvey has shown that the short-term enhancement of *P. candei*, observed by martins et al (2010) has been maintained over a 7 year period. Thus the simple approach of drilling pits in the rock is highly effective in promoting the abundance and biomass of this exploited species over many years; the abundance and biomass of *P. candei* 7 years on was at least 5 times greater in enhanced compared to control areas of the seawall.

As with results from the short-term experiment (Martins *et al*. 2010), limpets responded differently to the different habitat enhancement treatments. Observations after 7 years indicate that limpet abundance as a whole (not differentiating among different size classes; see Martins *et al*. 2010) was positively influenced by the abundance of larger pits, suggesting that the availability of large pits is potentially a limiting factor. This information can thus be used when designing new infrastructure; in order to enhance limpet stocks, emphasis should be placed on designing structures that offer a high density of pits of the larger size. It should be noted that the larger individuals in this study were all able to fit within the larger pits. It is unclear what happens to animals larger than those that fit into pits. Such larger animals may eventually seek other areas of the seawall as reliance on pits decreases with increasing

348 animal size (Martins *et al*. 2010). Such larger individuals are, however, uncommon on Azorean shores due to over-exploitation (Martins *et al*. 2008).

350

Community-wide effects

352 Even though the modifications made to the seawall were initially designed considering one specific species (*P. candei*), a longer-time perspective allows 354 examination of the influence on the structure of the entire assemblage, including littorinids, barnacles and macroalgae (see Fig. 4). When considering 356 littorinids, it is interesting to note that their response to the distinct treatments differed from that observed for limpets. While limpets appeared to be limited 358 by the availability of large pits, littorinids were more abundant in the smaller pits (see Fig. 4a). Their abundance also did not appear to be limited by the 360 density of pits in contrast to that found for limpets. This might reflect the gregarious nature of littorinids as several individuals of both *T. striatus* and *M.* 362 *neritoides* were often found sharing a single pit, as was also noted by Skov *et al*. (2011). This was uncommon among limpets that were generally found 364 inhabiting pits alone. This different behaviour between limpets and littornids likely reflects differences in the relative strength of intraspecific competition 366 among these gastropods (Underwood 1978).

368 Substantial variation in abundance of the other taxa (barnacles and macroalgae) was also observed among experimental treatments, especially in 370 relation to pit size (see Fig. 4a). This suggests that the modifications made to the seawall may have also influenced species other than prosobranch 372 gastropods. This is not surprising as surface topography is known to affect the

settlement by many organisms (e.g. Crisp 1955; Harlin & Lindbergh 1977;
374 Raimondi 1988). There is, however, an alternative explanation: that changes in the abundance of barnacles and macroalgae are an indirect effect of
376 treatments through changes in the structure of the grazer assemblage (e.g. Hartnoll & Hawkins 1985; Lubchenco 1983; Farrell 1988; Johnson *et al*. 1998;
378 Jenkins *et al*. 2005). For instance, ephemeral algae were generally more abundant in areas of the seawall enhanced with small pits. Although in such
380 areas there were also increased densities of littorinids, there was little difference in the community structure between these areas and the smooth
382 unmanipulated control areas of the seawall. This result suggests that littorinids have little influence on the overall structure of the community - as
384 noted also by O'Connor & Crowe (2005) and Griffin *et al*. (2010) - even though their abundance was enhanced by the addition of small pits. In
386 contrast, areas of the seawall enhanced by the addition of large pits supported the most distinct community structure with a comparatively higher
388 abundance of limpets, turfs and barnacles, and a lower abundance of ephemeral algae (Fig. 4a). Unlike ephemeral algae, a positive correlation was
390 found between barnacles and turfs and the abundance of limpets suggesting that the latter may facilitate their establishment. As is widely known, intertidal
392 limpets generally have a large negative effect on the abundance of ephemeral algae (Hawkins 1983; Van Tamelen 1987). Ephemeral algae, in turn, can
394 have an inhibitory effect of the establishment of perennial algae (e.g. Sousa 1979; Hawkins 1981; Viejo *et al*. 2008, Jenkins & Martins 2010). Selective
396 removal of ephemerals by high density of limpets in areas of the seawall enhanced with large pits may have thus indirectly facilitated the establishment

398 of barnacles and turfs (Hawkins & Hartnoll 1983; Van Tamelen 1987; Benedetti-Cecchi 2000) (Fig. 4b). Overall, these results appear to suggest
400 that the changes seen in the community structure in areas of the seawall enhanced with the addition of large pits are a result of modifications to the
402 network of interactions among intertidal species (as schematically represented in Figure 4b).
404

Conclusion

406 Our results suggest that the experimental modifications made to coastal engineering can have long-lasting effects. This result is important from a
408 conservation perspective and reinforces the concept that simple modifications made to coastal defence structures, that are unlikely to affect structural
410 integrity of the building blocks, can be used as a lasting and effective tool for the conservation of species, provided that a solid understanding of the
412 ecology of the focal species is known. While the enhancement of unprotected coastal infrastructures may be pointless, many infrastructures actually have
414 regulated access. In these cases, coastal infrastructures may positively influence stocks of important species but also impact nearby areas via spill-
416 over effects. Our results, however, also suggest that the modifications to the seawalls can influence non-targeted species both directly, by affecting the
418 spatial distribution of the organisms, and indirectly, by affecting the spatial distribution of competitors and predators. Understanding the interactions
420 between species can lead to a rule-based approach to interventions to enhance biodiversity.
422

ACKNOWLEDGMENTS

The initial experiment was supported by Fundação para a Ciência e Tecnologia (FCT) through a PhD grant awarded to GMM (SFRH/BD/22009/2005). During this experiment, GMM was supported by a post-doctoral grant awarded by FCT (SFRH/BDP/63040/2009). This research was partially supported by the European Regional Development Fund (ERDF) through the COMPETE and Operational Competitiveness Programme and national funds through FCT, under the project “PEst-C/MAR/LA0015/2011”. The authors would like to thank Eva Cacabelos and João Faria for help during fieldwork.

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Table 1. χ^2 test of independence comparing the mean abundance of grazers among treatments. χ^2 global = 30.26, d.f. = 4, $P < 0.001$

	Species of grazers		
Treatment	***P. candei***	***T. striatus***	***M. neritoides***
Large, High			
Observed	19.6	2.3	6.0
Expected	10.07	5.89	11.94
χ^2 contribution	9.03	2.19	2.96
Large, Low			
Observed	8.3	1.9	8.5
Expected	6.74	3.95	8.00
χ^2 contribution	0.36	1.06	0.03
Small, High			
Observed	8.5	6.9	16.7
Expected	11.58	6.78	13.74
χ^2 contribution	0.82	<0.01	0.64
Small, Low			
Observed	1.2	10.9	13.4
Expected	9.20	5.38	10.91
χ^2 contribution	6.96	5.65	0.57

642 Table 2. Pearson's product-moment correlation coefficients between the abundance of grazers and the sessile taxa in experimental enhanced areas of
644 the seawall.

	Barnacles	Turfs	Ephemerals
646 *P. candei*	+0.36	+0.36	-0.31
T. striatus	-0.03	-0.27	+0.08
648 *M. neritodes*	-0.16	-0.32	-0.20

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Figure caption

Fig.1. Mean (+SE) abundance each of the prosobranch gastropod species (a) *P. candei*, (b) *T. striatus*, (c) *M. neritoides* and (d) their combined abundance, in unmanipulated controls and habitat-enhanced areas of the seawall in November 2014. Abundance of enhanced areas of the seawall is averaged among all the four enhancement treatments. Data from the two sites was pooled together for clarity as there was no significant variation between sites (Table S1).

Fig.2. Mean (+SE) percentage cover of (a,b) barnacles, (c,d) corticated turfs and (e,f) ephemerals in November 2014. Comparison between unmanipulated controls and habitat enhanced areas of the seawall on the left (see legend on Fig. 1 for further details); comparison among different habitat enhancement treatments on the right. LH – Large pit size and High density, LL – Large pit size and Low density, SH – Small pit size and High density, SL – Small pit size and Low density. Data from the two sites was pooled together for clarity as there was no significant variation between sites in such most cases (Table S3).

Fig.3. Mean (+SE) each of the prosobranch gastropod species (a) *P. candei*, (b) *T. striatus*, (c) *M. neritoides* in each of the enhancement treatments in November 2014. The last panel (d) is a duplication of data from previous panels (without error bars for clarity) to show the relative differences in the abundance of all species in each treatment. As such, bar length corresponds

to the mean abundance of *Patella candei* (black), *Tectarius striatus* (grey) and
692 *Melarhaphe neritoides* (white). Legend as in Figure 2.

694 Fig. 4. a) Graphical representation of the community-wide effects of as a result of habitat enhancement treatments related to pit size as of November
696 2014. For each of the five taxa data were standardised as the mean/maximum abundance to represent magnitude of differences and to put abundance of the
698 different taxa at equal scale levels; continuous line – unmanipulated controls, small-dotted line – areas enhanced with small pits; long-dotted line – areas
700 enhanced with large pits. b) Conceptual representation of the possible network of interactions as result of habitat enhancement treatments (b1, b2
702 and b3). Continuous arrow – direct effect, dashed arrow – indirect effect. Arrow thickness indicates the relative strength of effect; ± indicates whether
704 effects are negative or positive.

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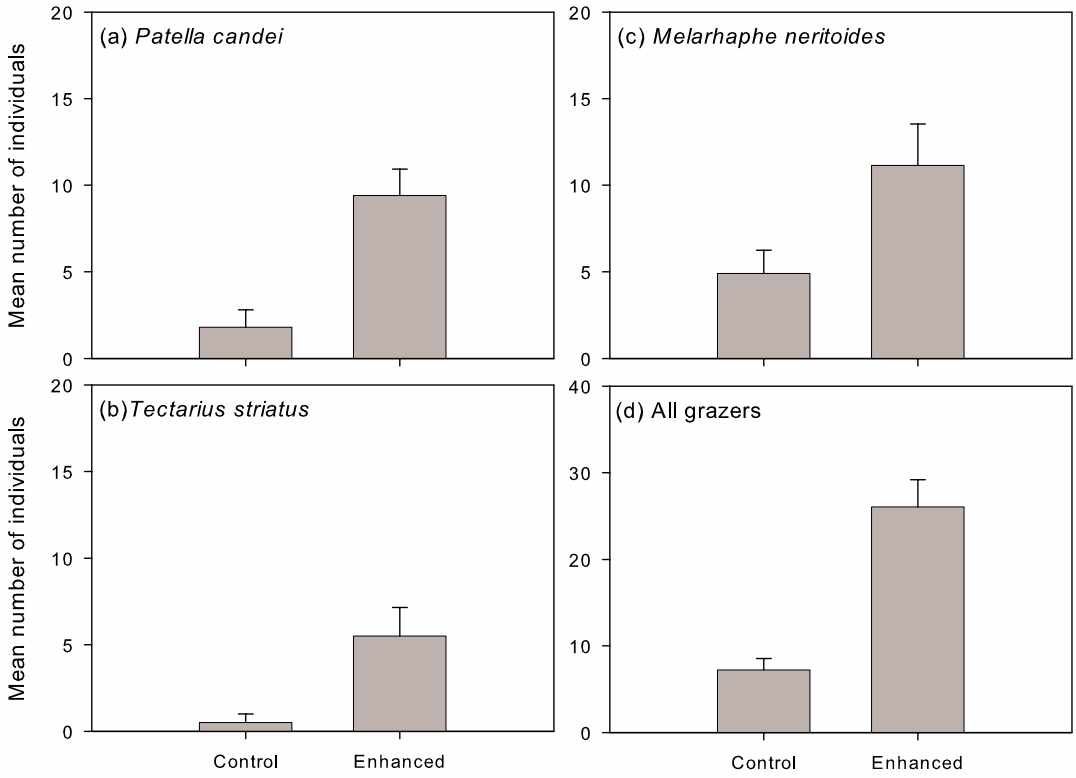

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Figure 1

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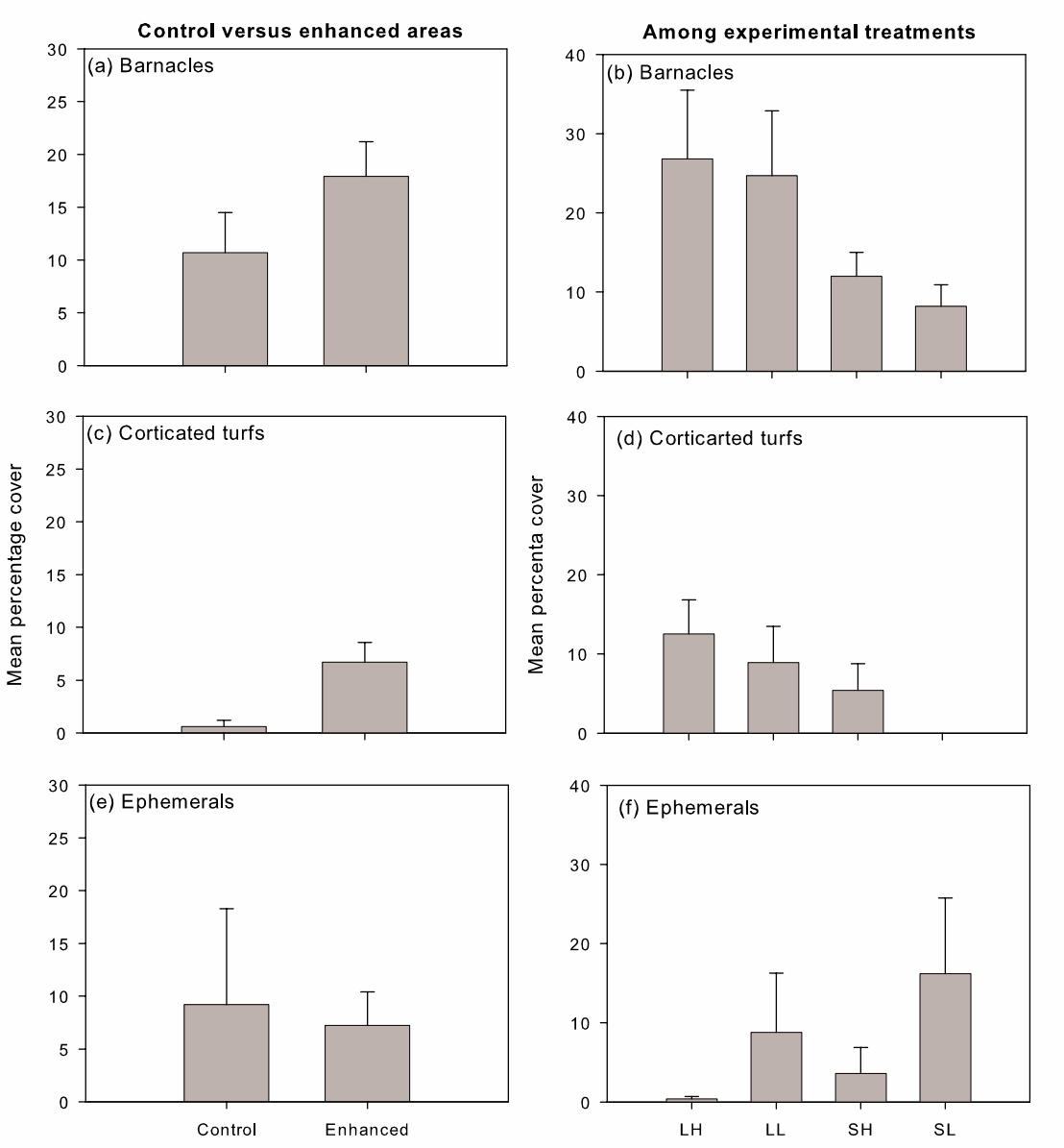

732 Figure 2

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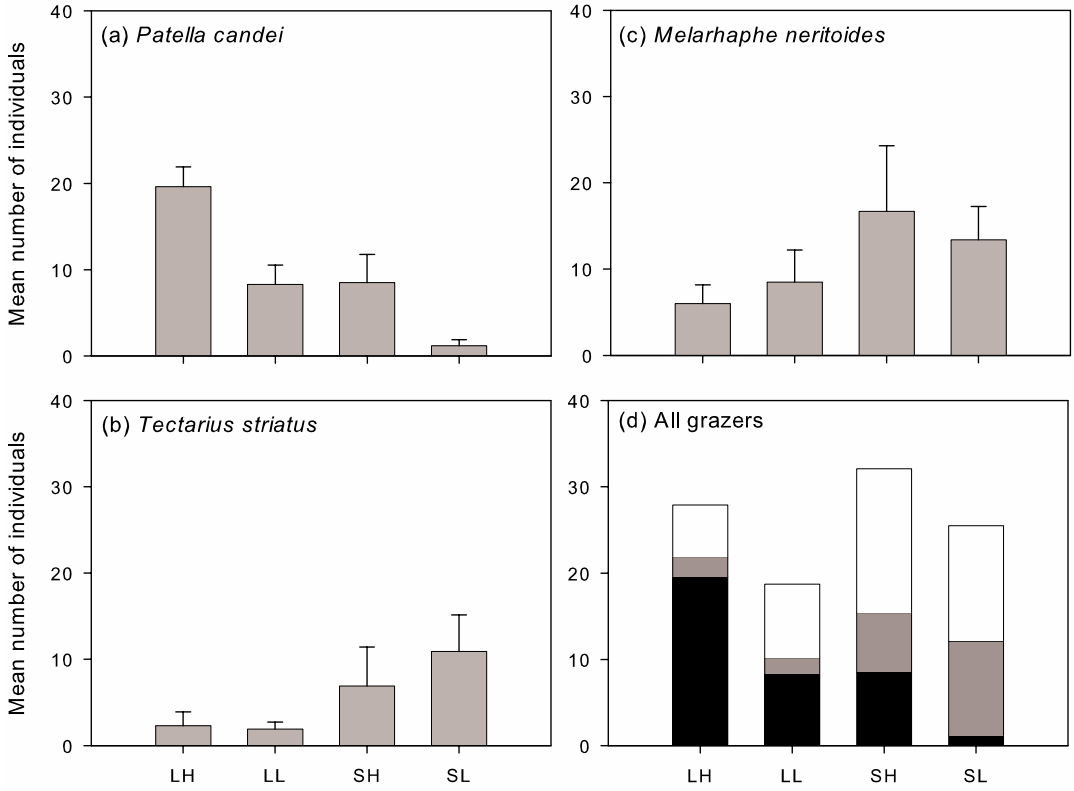

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Figure 3

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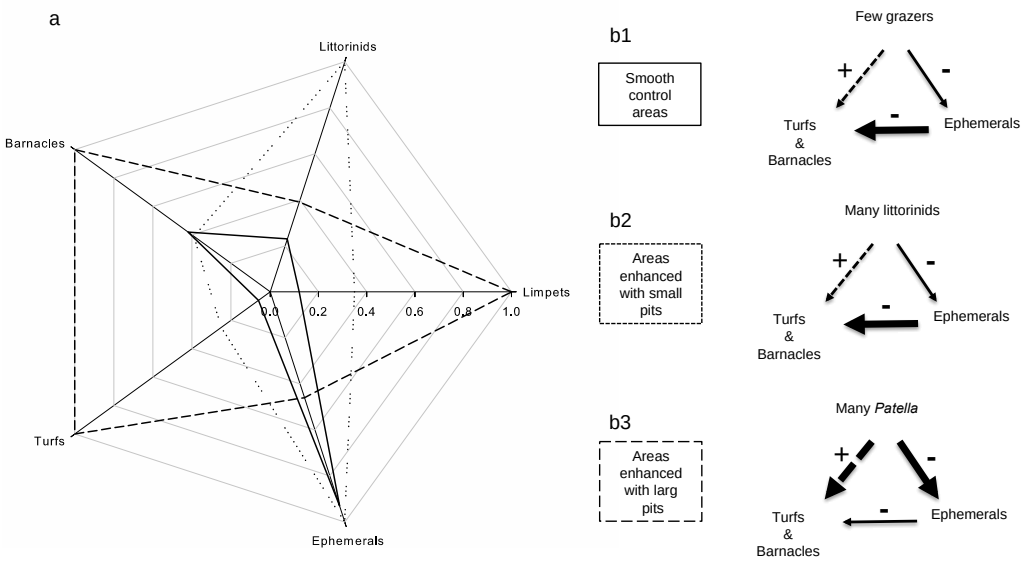
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Littorinids
Barnacles
Limpets
Turfs
Ephemerals
0.0
0.2
0.4
0.6
0.8
1.0
b1
Smooth control areas
b2
Areas enhanced with small pits
b3
Areas enhanced with larg pits
Few grazers
+
-
-
Turfs & Barnacles
Ephemerals
Many littorinids
+
-
-
Turfs & Barnacles
Ephemerals
Many Patella
+
-
-
Turfs & Barnacles
Ephemerals

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Figure 4